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ON *PATRO AUSTRALIS* WITH COMPARISONS OF STRUCTURE THROUGHOUT THE ANOMIIDAE (BIVALVIA)

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ABSTRACT

Study of specimens of *Patro australis* has involved further consideration of the Anomiidae,[1] in particular the extent of the differences between the more primitive *Pododesmus (Monia)* and the more modified *Anomia*. These are now extended to include comparisons of visceral structure. In *Pododesmus* the visceral mass surrounds the centrally placed byssal apparatus, the two (very similarly sized) gonads arranged in the same longitudinal plane. The greater effects of lateral compression in *Anomia* involve restriction of the visceral mass to posterior and ventral surfaces of the byssal apparatus with great reduction of the left gonad but extension of the right gonad into both right *and left* mantle lobes. The distinctive features of *Heteranomia* are seen to include enclosure of the base of the foot within the left gonad. *Patro australis* resembles *Anomia* in most respects, the major differences being conchological, but is adapted for life on a more uneven surface and under more turbid conditions.

INTRODUCTION

In a recent general account of the superfamily Anomiacea (Yonge, 1977), very significant differences in structure (although not in habit, both living closely applied to flat surfaces) were found between species of what proved to be much the less structurally specialized *Pododesmus (Monia)* and those of the much more highly modified *Anomia*. *Heteranomia* with much the same mode of life differs from both but primarily in ctenidial structure. *Enigmonia,* however, despite its remarkably modified form and unique mode of life—a kind of bivalve limpet spending much time out of water on leaves and stems in the extremely damp atmosphere of mangrove swamps—has the same basic structure as *Anomia*.

Patro australis (Gray) was also examined but only by way of empty shells obtained from the British Museum (Nat. Hist.). This species is stated by Iredale (1939) to occur all around the north of Australia but Beu (1967) extends this south to Victoria on the east. The observations of both were confined to shells, Beu stating of *P. australis* that "It appears that these forms occupy some situation where the shell is able to grow unrestricted." Personal conclusions were to the same effect, the area of byssal attachment being somewhat more limited than in *Anomia* spp., the valves much more irregular with the posterior margins raised clear of the surface to facilitate egress of faeces and especially pseudofaeces. A drawing was made showing this suggested posture (Yonge, 1977, fig. 21).

More recently four preserved specimens of this species have been obtained from the Australian Museum, Sydney. The locality and habitat, given on the label, are "Saibai Village, Saibai, Torres Strait, N. Queensland, muddy sand and rock flat in front of village. Low tide 7 July, 1976." This species was originally described by Gray (1847) from the collections of the "Fly" as *Anomia australis* and then renamed by him in his review of the "Anomiadae" (Gray, 1849) as *Patro elyros,* this corrected to *Patro australis* by Iredale (1939). All taxonomic data have been based on shell characters and the initial purpose of this study was to check differences in internal structure between this and other anomiids. This has inevitably involved some re-examination and comparisons of structure in *Pododesmus cepio, Anomia ephippium, A. simplex* and *Heteranomia squamula* (the four species earlier examined) with results which extend previously published conclusions (Yonge, 1977). Further data are provided about the nature and significance of structural modifications in the Anomiidae.

[1]As restricted to exclude *Placunanomia* and *Placuna* (Yonge, 1977).

ABBREVIATIONS USED IN THE FIGURES

a	anus
ad	adductor
adc	catch muscle of adductor
adq	quick muscle of adductor
aol	anterior outer ligament layer
aprl	anterior pedal retractor, left
aul	auricle, left
aur	auricle, right
bn	byssal notch
br	byssal retractor
by	byssus
cr	crurum
cs	crystalline style sac
ctl	ctenidium, left
ctr	ctenidium, right
f	foot
hg	hypobranchial gland
il	inner ligament layer
isl	boundary of inner shell layer
m	mouth
mbn	membrane around byssal notch
mi	mantle isthmus
obn	opening of byssal notch
ogl	oral groove, left
ogr	oral groove, right
pbr	posterior byssal retractor
pol	posterior outer ligament layer
pl	labial palps, left
pr	labial palps, right
u	umbo
v	ventricle
vg	visceral ganglion
vma	visceral mass, anterior
vmp	visceral mass, posterior
vmv	visceral mass, ventral

SHELL STRUCTURE

The shell in the Anomiacea is described by Taylor, Kennedy & Hall (1969) as consisting in the main of calcitic, foliated structure, the restricted inner shell layer (Fig. 3, isl) is of aragonitic, complex crossed-lamella structure, the muscle scars which they surround "leave a trace of aragonite, prismatic myostracum through the complex crossed-lamellar layer." Their observations were largely confined to species of *Anomia* but Beu (1967) finds that in the three species of *Patro* which he examined the here somewhat thicker right (under) valve is prismatic, a notable distinction from *Anomia.* He also notes that the shell in all these species is more inflated than in *Anomia* or *Pododesmus* (those of *Enigmonia* and *Placuna* even more flattened). He noted that the shells were usually "regularly subcircular with the left (upper) valve "slightly saddle-shaped." His largest specimen was 60 mm long with the right valve 2 mm thick. Of the four specimens here available, all were roughly circular in outline with the greatest diameters ranging from 18 to 45 mm. All were inflated. One, shown in Fig. 1, was attached to a stone to the rounded side of which it conformed although projecting marginally. The right valves of all were internally convex (Fig. 6) indicating a general tendency to settle on rounded rather than flat surfaces. The upward extensions of the posterior margin, although present, were not so well marked in these specimens as they were in the shell originally figured.

The upper surface of the left valve (Fig. 2) has what Beu describes as a "regular fine sculpture of radial ribs, of which every tenth is stronger than the others." Internally (Fig. 3) the restricted white inner shell layer down the centre is largely occupied by three large muscle scars, the most ventral that of the adductor, the other two those of the divided posterior byssal retractor. The larger (more dorsal) one (br), as in Anomiidae generally, is larger than that of the adductor (ad). In addition, just below the anterior margin of the resilifer, there is the scar of the small left anterior pedal retractor. Conditions here are similar to those in *Anomia* although, as Beu

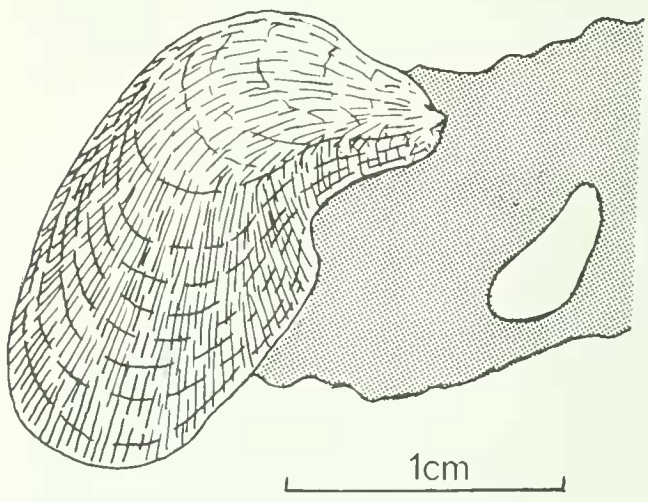

FIG. 1. *Patro australis,* animal attached to rounded surface.

points out, the three major scars are somewhat more vertically arranged; the anterior retractor scar (aprl) is also somewhat larger.

In *Pododesmus* the byssal retractor is only rarely divided. In *Heteranomia* the adductor and posterior pedal retractor scars merge into one as pointed out by Winckworth (1922) who separated the genus on this basis together with the distinctive ctenidia described by Ridewood (1903) and Atkins (1936).

The characteristic deep notch on the right valve is distinctly smaller in *Patro* than in spe-

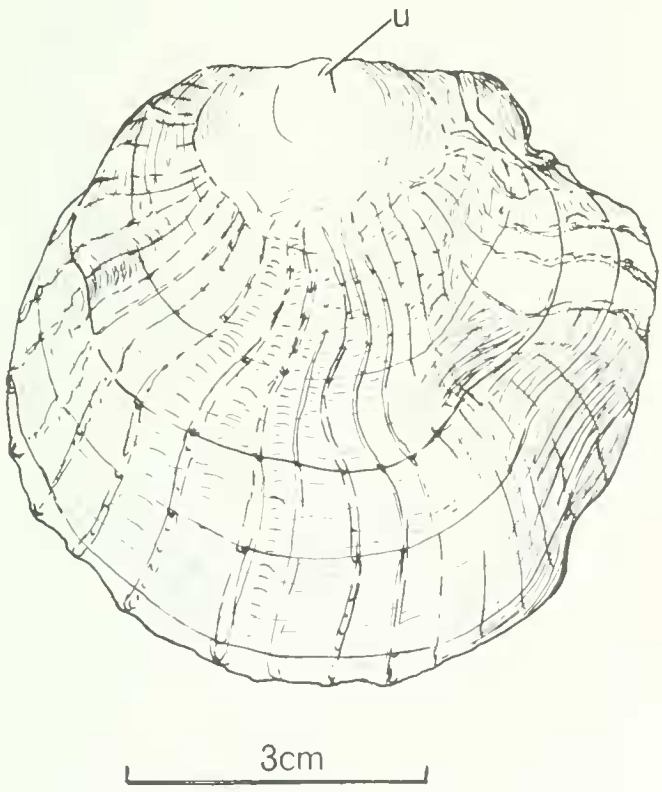

FIG. 2. *P. australis,* left valve, outer surface (from Yonge, 1977).

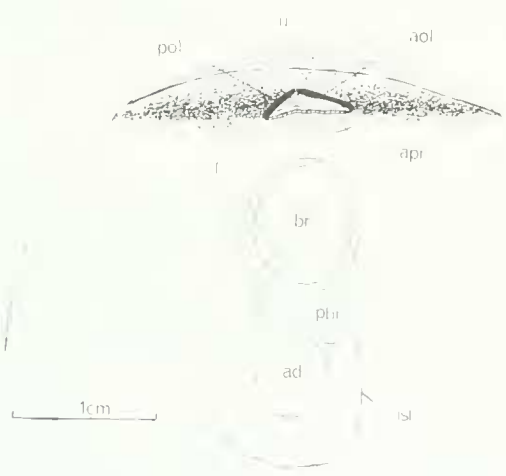

FIG. 3. *P. australis,* left valve, inner surface showing ligamental attachments (inner layer hatched, outer layers black) with inner shell layer containing three major muscle scars.

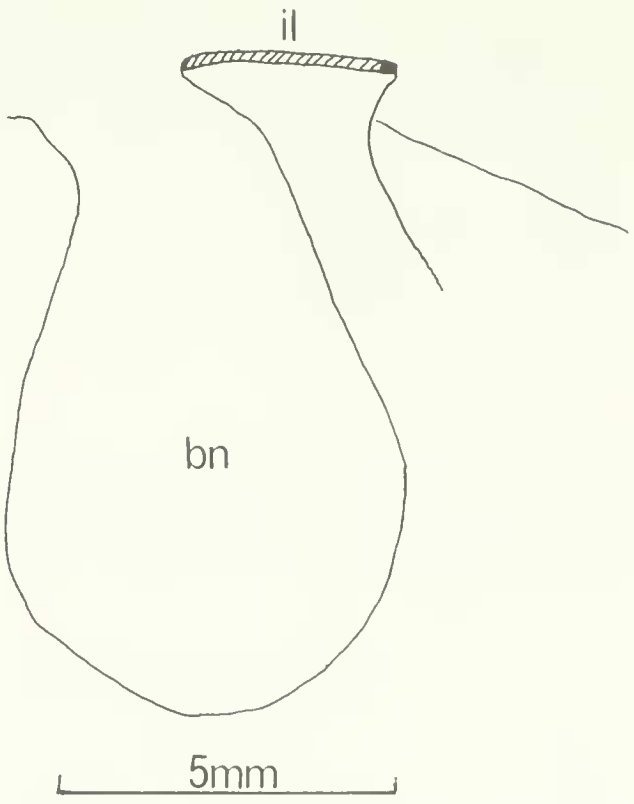

FIG. 4. *P. australis,* inner surface of dorsal region of right valve showing byssal notch with crurum and attachment of inner ligament layer.

cies of *Pododesmus* and *Anomia.* Moreover, as shown in Figs. 4–6 the notch is always wide open which is not true for either of the other genera where it is often completely closed by approximation, and sometimes fusion, of the anterior margin with the crural area. There also the calcified byssus may become fused with the margins of the notch (or foramen as it may become). There is no evidence that this happens in *Patro* where the animal has a more restricted area of attachment. The subcrural groove on the under face of that structure (permitting dorsal extension of byssal fibres) which is so very well marked in *Pododesmus* (Yonge, 1977) is absent in *Patro* and there is no attachment of a right anterior pedal retractor to the inner base of the crurum. The only muscle scar on the right valve is that of the adductor. In all three respects *Patro* resembles *Anomia.*

LIGAMENT

Owing to the extent to which the left valve overarches the right valve dorsally, the ligament in the Anomiidae is vertically instead of laterally disposed. It is topographically extended horizontally, parallel to the substrate.

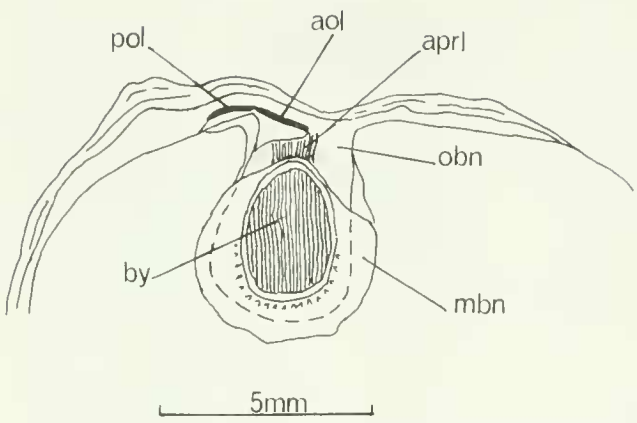

FIG. 5. *P. australis,* intact animal, under (right) view of byssal region showing widely open byssal notch with united anterior and posterior outer ligament layers on under (outer) side of crurum.

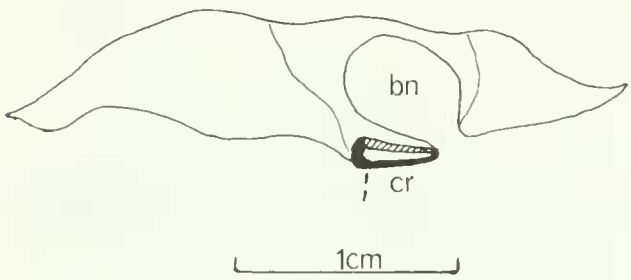

FIG. 6. *P. australis,* right valve viewed from dorsal aspect showing convex form also crurum with complete oval-shaped ligament, position of union of anterior and posterior outer layers indicated by broken line.

As previously shown (Yonge, 1977) this overarching by the left valve involves a "supradorsal" extension of the mantle margins at both ends of the ligament. This results in secretion of shell *outside* the ligament and consequent displacement of the umbo from the margin (Fig. 7). At the same time the anterior and posterior outer (lamellar) ligament layers are bent back topographically below the inner ligament layer secreted by the mantle isthmus (Figs. 3–6).

Conditions on the right (under) valve are profoundly influenced by the presence of the relatively enormous anomiid byssal notch which, as shown in Figs. 4 and 6, stretches within and to the anterior of the ligamental region. In consequence on this valve the resilifer surface occupies the summit of a unique anomiid type of chondrophore known as a crurum. In side view this is straight both in *Patro* (Fig. 4) and *Anomia,* unlike *Pododesmus* where it is convex. Although there cannot be supradorsal extension of the shell on this side, the outer ligament layers (secreted by epithelia which stretch between the valves) are inevitably bent in an oval around the topographically under side of the crurum. The resultant form of the ligament is best realized by viewing a right valve from the dorsal aspect (Fig. 6). The flat resilifer surface of the crurum bears the inner ligament layer (il) on its upper (i.e. interior) surface and the united anterior and posterior outer layers (ad, pol) on the lower (i.e. outer) surface. In life these layers are, of course, continuous with those on the upper, left valve shown in Fig. 3.

Conditions, however, are somewhat more advanced in *Patro* than *Anomia,* indeed there is an interesting gradation of ligamental structure starting with that in *Pododesmus* and indicated semi-diagrammatically in Fig. 7. In *Pododesmus* (A) initial supradorsal extension of the mantle margins and so of the outer valve layers they secrete is followed by their retreat with later decay of this region. This involves breakdown of the shell marginal to

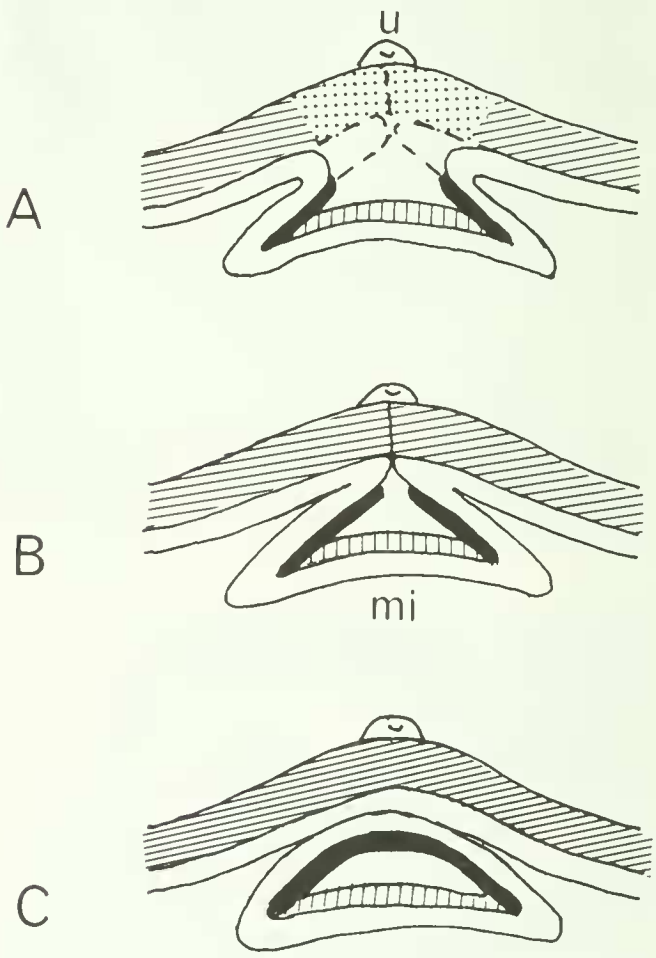

FIG. 7. Diagrams comparing ligamental conditions in:— A, *Pododesmus,* incomplete supradorsal extension followed by decay and exposure of dorsal surface of ligament; B, *Anomia,* complete supradorsal extension with fusion of shell but not of outer layers of ligament; C, *Patro,* complete fusion of ligament as well as shell.

the umbo and of the upper regions of the exposed ligament (described and figured in Yonge (1977) and indicated in Fig. 7A). In *Anomia* (B) the initial supradorsal growth of the mantle margins endures with union of the tissues and so persistence and increase of shell marginal to the umbo. The ligament remains enclosed but the anterior and posterior outer layers do *not* unite; there is always an appreciable gap between them. This is *not* the case in *Patro* (C) (or in *Enigmonia* and *Heteranomia*) where there must be more complete union of the mantle margins resulting in disappearance of the line of union between the supradorsal regions of the shell which persists in *Anomia* (B). Fusion of the outer ligament layers produces the complete compressed oval shown in Fig. 6. The anterior outer ligament layer is appreciably the longer (Figs. 3, 6).

Because not specifically considered previously (Yonge, 1977), the periostracum needs mention. In *Placuna* this becomes separated from the inner and outer layers which form the primary ligament to produce a highly significant secondary ligament. This extends along the new hinge line evolved in association with the change in that genus from byssal cementation to unattached life on mud. It is concerned with alignment of the valves, the primary ligament solely with provision of the opening thrust. But in *Patro,* as in all the Anomiidae, although the periostracum loses contact with the ligament when the mantle margins overarch to unite temporarily or permanently, it retains contact with the margin of the left valve which now extends around the entire periphery, periostracum everywhere forming its outermost layer. There is no production of, or need for, a secondary ligament.

INTERNAL STRUCTURE

Comparison between *Anomia* and *Pododesmus.* Before the smaller differences between *Patro* and *Anomia* can profitably be discussed, more needs to be said about the differences between *Anomia* and *Pododesmus*. There has been some unfortunate confusion here because species of these two genera have been examined from different aspects and never directly compared except incompletely by the writer (Yonge, 1977). *Anomia ephippium* has been the subject of detailed anatomical studies by Lacaze-Duthiers (1854), Pelseneer (1891, 1911) and Sassi (1905) with further observations on *A. glabra* by Jackson (1890), *A. achaeus* by Pelseneer (1911) and *A. cytaeum* by Tanaka (1955). Structure in this genus has been thoroughly studied but there are no observations in life. All these workers apparently considered species of *Pododesmus (Monia)* as essentially similar in internal structure. Separation of the genera was based purely on conchological differences.

The state of affairs is just the opposite with *Pododesmus.* No study of internal anatomy has been made of any species but detailed observations have been made in life of the exposed mantle cavity with figures showing the organs and the course of ciliary currents on ctenidia, palps, mantle and visceral mass in *Pododesmus cepio* (= *Monia machrochisma*) (Kellogg, 1915; Yonge, 1977) and for *"Monia" squama* by Atkins (1936) who also examined and figured *Heteranomia squamula* (see below). During the years Atkins worked on these animals at Plymouth she reports never seeing specimens of *A. ephippium* and clearly assumed that it did not differ significantly in structure from *"Monia."* The present author also failed to see living species of *Anomia,* relying in his work on the Anomiacea on preserved specimens of *A. ephippium* from the west of Scotland and of *A. simplex* from the Atlantic coast of North America. Major differences were found between the two genera with *Pododesmus* decidedly the less modified and these were displayed in tabular form (Yonge, 1977, Table 1, p. 495). However the full extent of these differences was not appreciated.

These, largely affecting the distribution of the visceral mass, became apparent in the course of the present study and are best appreciated by reference to Fig. 8. After careful removal from the shell, preserved specimens of small *Pododesmus cepio* and *Anomia simplex* were embedded in 20% gelatin. After some hardening in 10% formalin these were cut horizontally through the centre of the foot and so of the byssal retractor (A, B) with the ventral portion later cut transversely thus passing through the ctenidia and ventral half of the byssal retractor, single or divided (A_1, B_1). Differences in the disposal of the visceral mass, especially of the gonad, then became apparent.

Differences in the degree of supradorsal extension have already been noted (Fig. 7, A, B) while the presence of the very large hypobranchial glands separating the ctenidia in

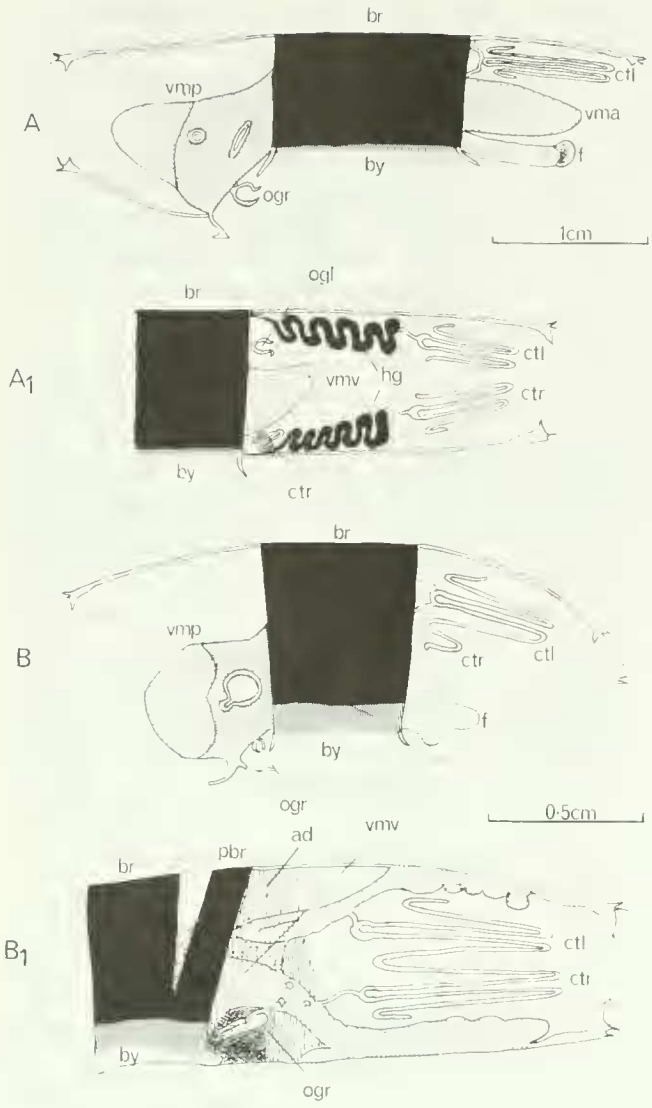

FIG. 8. *Pododesmus cepio* (A) and *Anomia simplex* (B), horizontal (A, B) and transverse (A_1, B_1) sections through gelatin-embedded specimens (for details see text). Digestive diverticula indicated by fine, and gonad by coarse, stippling.

Pododesmus but absent in *Anomia* is further demonstrated in these sections (Figs. $8A_1$, hg; $8B_1$). In the latter, also, the ctenidia are seen to be united in the middle line by tissue instead of by the ciliary junctions that connect those of *Pododesmus* for a short distance anterior to the hypobranchial glands. As already figured (Yonge, 1977), the ctenidia which in *Pododesmus*, as in bivalves generally, pass symmetrically to the right and left palps, in *Anomia* and *Enigmonia* are asymmetrically disposed. As shown for the similar *Patro* in Fig. 9, three demibranchs make functional contact with the left (upper) palps and only one with the right palps. This difference also is shown in Fig. 8 (cf. A & B, ctl, ctr).

These gelatin sections further reveal that in *Pododesmus* the visceral mass, including the gonads, although laterally much compressed, remains in the mid-line more or less symmetrically disposed around the byssal apparatus. Held in position between right and left anterior pedal retractors, the mouth continues to be centrally placed, the gut surrounded by the digestive diverticula extending along the posterior surface of the byssal apparatus with the anus as usual projecting at the end of a short rectal extension on the hind surface of the adductor. The very long separate style sac, characteristic of the Anomiacea, extends into the substance of the right mantle lobe. Full effect of lateral compression is shown by the gonads, although remaining approximately the same size, the left gonad extends around the anterior and then ventral surfaces of the byssal apparatus (Fig. 8A, vma; A_1, vmv), initially passing between the left ctenidium (ctl) and the foot (f). The right gonad surrounds the digestive diverticula on the posterior side reaching down below the level of the byssal apparatus and meeting, but not uniting with, the left gonad. The two gonads therefore encircle the central mass of the byssal apparatus on the anterior (vma), ventral (vmv) and posterior (vmp) sides. There is the minimum of change from the normal bilateral symmetry of the Bivalvia.

Conditions are very different in *Anomia*. As described in *A. ephippium* by Lacaze-Duthiers (1854), Pelseneer (1891) and in greatest detail by Sassi (1905) the effects of lateral compression are much greater. The visceral mass is almost entirely concentrated on the posterior side. The gonads are extremely asymmetrical, that on the left greatly reduced and confined to the dorsal side of the byssal apparatus, while that on the right is hypertrophied and extended by way of three connexions from the visceral mass, widely throughout the right mantle lobe. According to Sassi (1905) the former opens dorsally into the left kidney, which encircles the byssal apparatus, the latter into the right kidney postero-ventrally.

Examination of *A. simplex* largely confirms these statements. With loss of the right anterior pedal retractor the mouth moves from the central to a more posterior position (as shown for *Patro* in Fig. 9A, m). The rectum gets caught up with the right gonad so that the anus becomes attached to the right mantle lobe instead of projecting freely into the mantle cavity. As shown in Fig. 8B, the visceral mass does not extend anteriorly between ctenidia and foot. It is confined to the posterior and ventral region (vmp, vmv). It is largely

occupied by the hypertrophied right gonad which extends beyond it mainly into the right, but also to some extent into the left, mantle lobe. The common origin of the gonadial tissue in both lobes, coming from the ventral region of the visceral mass is clearly shown in Fig. $8B_1$. This extension of the right gonad into the left lobe, the left gonad much reduced, represents a unique attempt to reestablish functional bilateral symmetry in these extremely asymmetrical bivalves. There is no evidence that this occurs in *A. ephippium* but this may be because only young animals have been examined. As noted later there is some evidence that penetration into the left mantle lobe is beginning to take place in one specimen of *Patro,* all of which were small. Conditions are very different in other anomiaceans, in *Enigmonia* the left gonad is much the larger (Bourne, 1907) while in *Placuna* it is lost (Hornell, 1909).

Comparisons between *Heteranomia* and other genera. Ridewood (1903) in his survey of lamellibranch gills showed that *"Anomia aculeata,* Muller" (= *Anomia squamula* Linnaeus) has unreflected ctenidial filaments. He therefore associated it with *Dimya* in a distinctive order Dimyacea. Its obvious anomiid affinities were later recognized by Winckworth (1922) who erected the genus *Heteranomia* for its accommodation. Recent examination of the filaments in the Dimyidae (Yonge, 1978) shows the ctenidial resemblance to be superficial, the inner filaments of the two sides being united in different manners. In the Dimyidae also, unlike *Heteranomia,* the outer demibranchs make no functional contact with the mantle surface. No work has been done on internal structure in *Heteranomia* but Atkins (1936) described and figured superficial anatomy.

It was earlier shown (Yonge, 1977) that *Heteranomia* resembles *Anomia* in possession of a straight crurum without a right anterior pedal retractor. The rounded byssal notch has more resemblance to that of *Pododesmus* in possession of a very small subcrural groove. Supradorsal fusion of the tissues is complete and with the outer ligament layers united as they are in *Patro.* There is also a symmetrical secondary union of the mantle lobes posterior to the ligament (i.e. *unlike Anomia, Patro* and *Enigmonia* where it is asymmetrical) and, as shown by Atkins, this union extends over the greater part of the exhalant region unlike the other genera.

Further examination in the light of the present work shows that although the right pedal retractor is lost the mouth remains in much the same position as in *Pododesmus*; there is a large left anterior retractor as figured by Atkins. The gonads are disposed essentially as in *Pododesmus* without any intrusion of the right gonad into the mantle. A unique feature is the enclosure of the basal half of the foot in the left gonad. This probably reduces pedal activity in cleansing and may be correlated with the greater sweep of the unreflected ctenidia. The adductor is smaller than in other anomiids, its scar, as noted by Winckworth (1922), blending with that of the very much larger, undivided byssal retractor.

In brief, in its anatomy *Heteranomia* has affinities with *Pododesmus* (visceral mass, position of mouth), with *Anomia* (straight crurum, complete supradorsal fusion of tissues), with *Patro* (union of outer ligament layers) together with features peculiar to itself (unreflected ctenidia, enclosure of base of foot within right gonad). This is a very well defined genus.

Structure in *Patro australis*. The general appearance after removal from the shell and viewed from the right (under) and left sides is shown in Fig. 9A, B. Structure is similar to that of *Anomia* and *Enigomia* with the three demibranchs associated with the left labial palps (pl), and the mouth (m) well over on the right side following loss of the right anterior pedal retractor. The anus (a) at least in this small specimen (because conditions might change with growth) is not adherent to the right mantle lobe. The left anterior pedal retractor (aprl) is larger than in *Anomia* spp. The visceral mass is confined to the posterior and ventral sides of the central byssal apparatus with the right gonad extending widely throughout the right mantle lobe. In this the attenuated style sac (cs) describes a complete circle. Only in one, rather larger specimen, was there some indication of extension of this gonad into the left mantle lobe.

In the absence of a pericardium, the ventricle (v) with the asymmetrical entering auricles (aur, aul) are freely exposed. Viewed from the right side (B) the four muscles producing the scars shown in Fig. 3 are apparent. As throughout the Anomiacea, only a small section of the adductor is composed of nonstriated catch muscle (adc). Adduction is achieved by way of the much larger divided byssal retractor (br, pbr) the quick muscle of the adductor (adq) being responsible for ejection of pseudofaeces by way of the somewhat

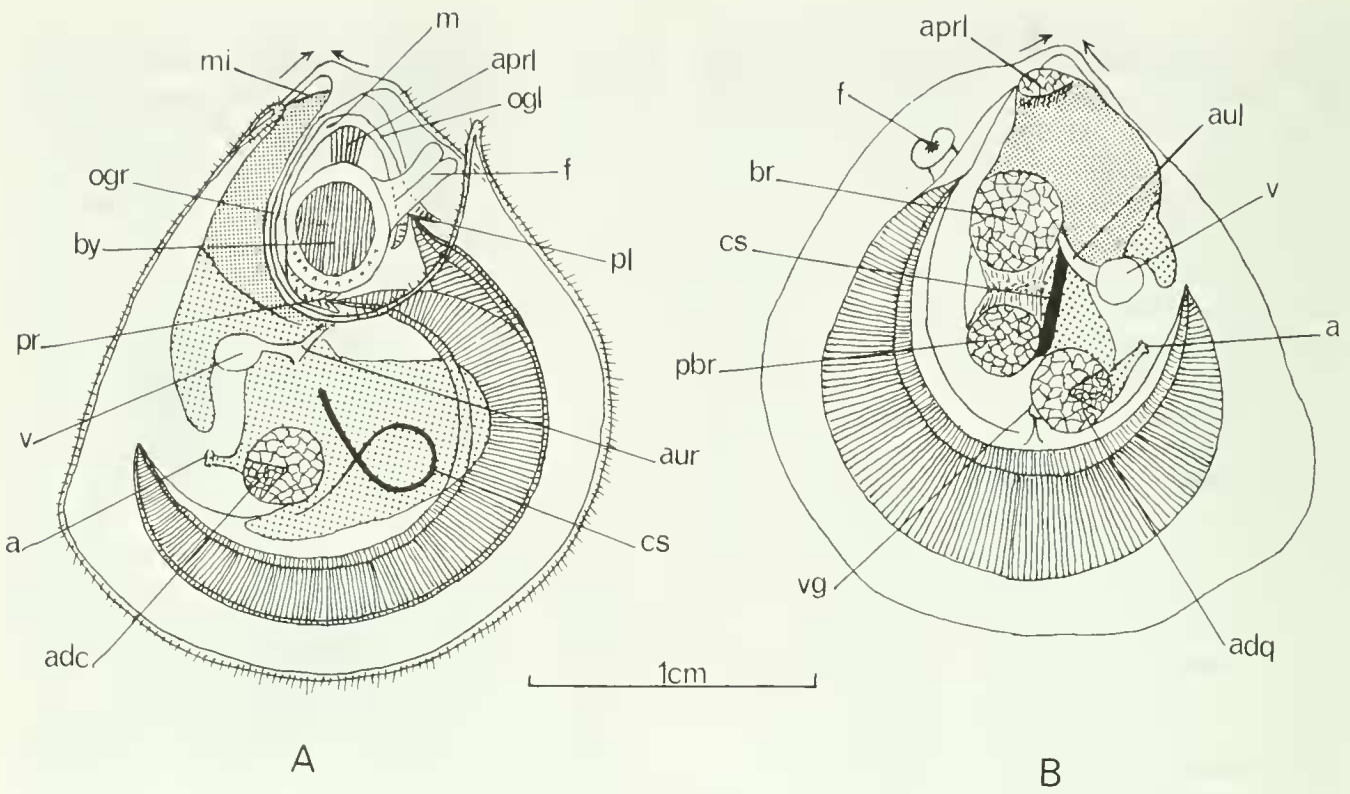

FIG. 9. *P. australis,* specimen removed from shell and viewed A, from right (under) side and B, from left side. Arrows indicate supradorsal extension at each end of mantle isthmus resulting in fusion above. Digestive diverticula and gonad indicated as before.

raised posterior region of the mantle cavity. Although only seen after preservation when much contracted, the foot does appear to be smaller than in *Anomia* sp. and so of possibly less importance in cleansing.

The major differences between *Patro* and *Anomia* are conchological, the prismatic character of the right valve, the smaller and more open byssal notch (Fig. 5), the complete union of the outer ligament layers (Fig. 7C) and the uneven convexity of both valves (Fig. 6). The area of byssal attachment is somewhat smaller but not less calcified. This, together with the obvious ability of the valves to conform to irregular surfaces, supports the opinion of Beu (1967) that species of this genus are adapted for life on more irregular surfaces than those of other anomiid genera. A greater capacity for dealing with sediment is also indicated. Thus, although regarded as a subgenus of *Anomia* in the *Treatise on Invertebrate Paleontology,* there is good evidence for regarding *Patro* as a distinct genus, very closely related to *Anomia* but with its species capable of exploiting the possibilities of life on more irregular substrates and under more turbid conditions.

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